

BY BRYAN PATTERSON

INTRODUCTION

The history of this peculiar group of mammals was ostensibly a blank until 1937, when Broom described an extinct species of *Elephantulus* from the Pleistocene of South Africa. Four extinct genera, however, had been described earlier, from 1910 on, but, having been placed incorrectly in other groups of mammals, had gone unrecognized. One of these, *Palacothentoides* Stromer, has been detected as a macroscelidid by Butler and Hopwood (1957); the other three, *Metoldobotes* Schlosser, *Myohyrax* Andrews and *Protypotheroides* Stromer are here placed in the family for the first time. *Palacothentoides* was originally described as a marsupial, *Metoldobotes* as a mixodeetid insectivore, and *Myohyrax* and *Protypotheroides* as hyracoids. So extraordinary a situation is, I believe, without parallel in mammalian paleontology.

This paper came into being in a rather roundabout way. Creatures with names such as *Palacothentoides* and *Protypotheroides* have a certain fascination for anyone with a taste for South American fossil mammals. Being in Europe during the spring of 1957, I took the opportunity of visiting Munich and examining material of both forms. The collection included an important undescribed specimen of *Palacothentoides africanus*, and this I was very kindly permitted to borrow for further study. Shortly after completing the description of it, and with the details of macroscelidid dental structure fresh in mind, I had occasion to consult Schlosser's memoir (1911) on Fayum mammals during a discussion of the dental formula of *Parapithecus*. There, staring up from the plate, was *Metoldobotes*, an obvious macroscelidid. (Discussions of *Parapithecus* are perennial; it is gratifying to be able to report this useful by-product of one of them.) On examining *Protypotheroides beetzi* in Munich I had noted a decided resemblance to *Palacothentoides*, but at the time had considered it to be an interesting example of convergence, one about on a par with the resemblance to the interatherid typotheres. It was only after consulting Whitworth's study (1954) of the Miocene hyracoids of Kenya in quite another connection that I began to suspect the Myohyracinae really were macroscelidids, a suspicion that hardened to conviction upon examination of Stromer's figures (1926) of posterianal remains from the Miocene of Southwest Africa. Here was a group

of elephant shrews that had masqueraded as ungulates for half a century. Broom's (1948) *Mylomys spiersi* from the Pleistocene, a form with hypsodont, rodent-like cheek teeth, revealed the former existence of yet another phylum of the family. It became clear that the surviving forms give little hint of a rather remarkable radiation that went on within the African continent throughout much of the Cenozoic. There is nothing remotely primate-like about the extinct phyla so far known. The fossil record in fact very definitely supports those who have been unable to accept the hypothesis of a close relationship between the elephant shrews and the treeshrews. As LeGros Clark has well put it (1959, pp. 318-319n): "In retrospect it is difficult to understand this taxonomic association . . . the differences . . . are so marked as to make it clear that they are really quite divergent types."

This study has been aided by National Science Foundation Grants G-3120 and GP 1188, which made it possible for me to examine specimens in Europe and in Kenya. For access to material I am indebted to the authorities of the British Museum (Natural History) and of The American Museum of Natural History, to Dr. Richard Dehm and to Dr. L. S. B. Leakey. Miss Margo Hayes has assembled the final manuscript and assisted in checking localities and references. The photographs are by Mr. Frank White and the drawings by Mrs. Dorothy Marsh. Figures of fossil macroscelidids are widely scattered in the literature and a number of them are in rather rare publications. Those pertinent to the work are accordingly redrawn here. Publication has been aided by National Science Foundation Grant GB-500.

TAXONOMY AND MORPHOLOGY

MACROSCOLIDIDAE

MACROSCOLIDINAE

METOLDOBOTES Schlosser

Metoldobotes Schlosser, 1910, p. 507; Matthew, 1910, p. 702.

Metolbodotes Schlosser, 1911, p. 70; Matthew, 1915, p. 467.

Type species: M. stromeri Schlosser, 1910.

Distribution: Early Oligocene, north Africa.

Emended diagnosis: I_3 (?), C, P_4 , M_2 . I_3 not bifid, with pronounced vertical groove on lingual side; C bluntly pointed, three sided; P_{1-3} short relative to $P_4 - M_2$; P_1 single rooted, roots of P_2 very closely appressed, P_3 with small anterior and posterior cusps, without posterior accessory cusp; P_4 and lower M with crista

obliqua running to posterior face of trigonid, talonid of M_3 short relative to trigonid. Horizontal ramus of mandible relatively short, deep; ascending ramus steep; symphysis long, extending to P_3 .

METOLDOBOTES STROMERI Schlosser

(Fig. 1 c, d)

Metoldobotes stromeri Schlosser, 1910, p. 507; Matthew, 1910, p. 702.

Metoldobotes stromeri Schlosser, 1911, pp. 70-72, 147, 157, 163, 164; pl. 9, fig. 5.

Type: An incomplete right horizontal ramus in the Stuttgart collections, with I_3 , C, $P_3 - M_2$, alveoli for I_2 , P_1 , roots of P_2 .

Hypodigm: Type only.

Horizon and locality: Fluvio-marine series, early Oligocene; Fayum, Egypt.

Diagnosis: As for the genus. The fragmentary type specimen appears to represent an animal somewhat larger than *Rhynchocyon petersi* and *Protyphotheroides bectzi*, and hence the largest known member of the family.

Discussion: *Metoldobotes*, with the exception of brief comments by Matthew and passing mentions in various editions of Zittel, has remained essentially unnoticed in the literature since its description. Schlosser tentatively assigned it to the Mixodectidae, a reference which, as Matthew (1915, p. 467) stressed, had nothing to recommend it in the way of positive resemblances between the Fayum form and any mixodectid.

The type ramus, incomplete anteriorly, preserves, in series, an anterior alveolus, an incisor, a partially erupted, conical tooth, the alveolus of a single-rooted tooth, the very closely appressed roots of a double-rooted tooth and the last four cheek teeth. Schlosser interpreted this array as $I_{1,2,3}$, C, $P_{3,4}$, $M_{1,2,3}$, but he made no comparisons with any macroselidid. Inspection of his figures at once reveals an impressive number of resemblances to the various members of this family, and suggests that the dental formula is in reality $I_{(1),2,3}$, C, $P_{1,2,3,4}$, $M_{1,2}$, as in *Rhynchocyon*, *Petrodromus*, *Elephantulus*, *Macroselides*, and *Myomygale* (an alveolus for I_1 in this interpretation is lacking, but the specimen is incomplete anteriorly). In the ensuing remarks the teeth will be so designated.

The crown of I_3 is described by Schlosser as being about half the height of the root; this is true of the incisors of macroselidines. A groove is present on the lingual faces of the incisors of members of this subfamily, although in no case is it as pronounced as shown in Schlosser's figure. The canine in *Rhynchocyon* is sometimes (e.g. MCZ 38782), although by no means invariably, not fully

erupted until after the posterior cheek teeth have come into wear. P_1 is single-rooted in *Macroscelides*, *Myiomygale*, and in some species of *Elephantulus*¹. The roots of P_2 are closely appressed in *Macroscelides*. P_3 of *Metoldobotes* resembles that of all members of

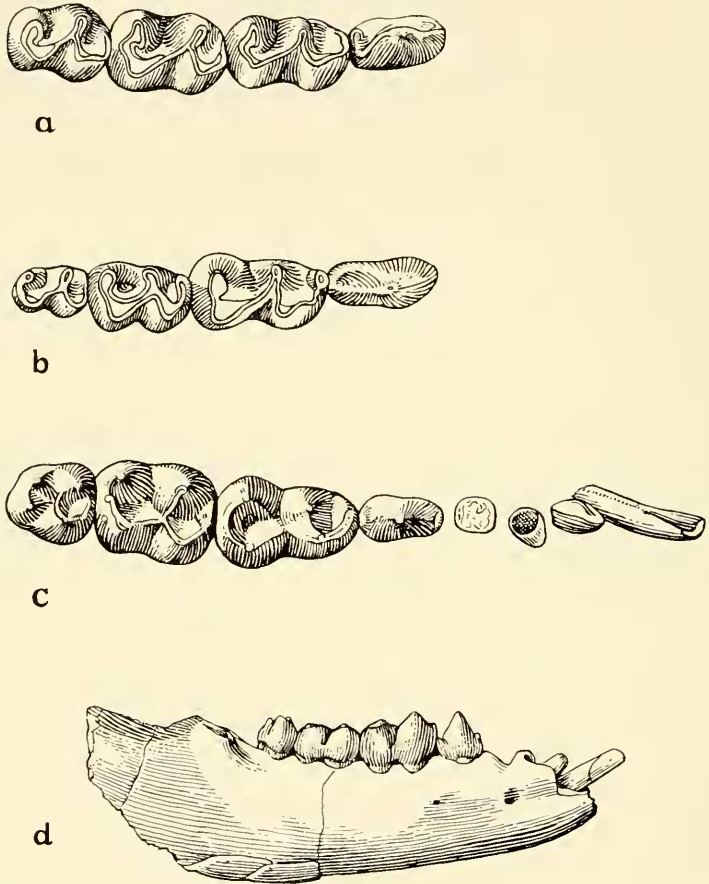


Figure 1. *c, d*, *Metoldobotes stromeri*, crown view of dentition and lateral view of mandible, *c* $\times 3$, *d* $\times \frac{3}{2}$; redrawn from Schlosser. *a*, *Petrodromus nigriseta*, MCZ 22434, *b*, *Rhynchocyon petersi*, MCZ 22573, crown views of $P_3 - M_2$, not to scale.

¹ Among the *Elephantulus* material in the Museum of Comparative Zoology collections I have found P_1 to be single rooted in *E. ovalaris* (29 specimens), *rufescens* (6), and *pulcher* (6); variable in *rupestris* (3 single and 3 double); and double rooted in *intufi* (5), and *fuscipes* (2).

the family in its proportions relative to $P_4 - M_2$ and in its possession of low anterior and posterior cusps, and that of the macroscelidines in the absence of an accessory cusp on the posterior slope of the protoconid. The large P_4 has a wide molariform talonid and a narrower, elongate trigonid. The tooth is typically macroscelidid in these features, and also as regards size relative to the molars and the structure and arrangement of the cusps and crests. The molars of *Metoldobotes* resemble those of the living macroscelidids in the nearly equal heights of the trigonids and talonids, the metaconids and entoconids higher than the protoconids and hypoconid, the absence of labial and lingual cingula and the structure and positions of cusps and crests generally. The paraconid is median, as in the macroscelidines. The crista obliqua runs to the center of the posterior face of the trigonid, as in the Miocene *Rhynchocyon clarki* (Butler and Hopwood, 1957, p. 10), rather than to the metaconid, as is the case in living forms. The relative lengths of M_1 and M_2 are approximately as in *Rhynchocyon*, and the talonid of M_2 appears to be about as small and short relative to the trigonid as in *R. cirnei* (e.g. MCZ 43735). In agreement with *Rhynchocyon* and the macroscelidines, the mental foramina are beneath P_{1-2} and P_4 ; the ascending ramus, to judge from Schlosser's figure, arises abruptly well behind the last molar. The masseteric fossa is shallow and, as in macroscelidines, extends down to the level of the tooth row. The horizontal ramus is deeper than in either the Rhynchocyoninae or the Macroscelidinae, shallower than in the hypsodont Myohyracinae. That part of the tooth row anterior to P_4 is somewhat shorter relative to the length of the series as a whole than in living members of either of the first two subfamilies, but is approximately comparable to *Myohyrax* and *Mylomysgale* in this respect. The symphysis, *vide* Schlosser, extends to P_3 (his P_4) and is hence longer than in all other known members of the family, in which it terminates beneath C or P_1 .

On the evidence available it is difficult to assign *Metoldobotes* to subfamily with any confidence. The Fayum form does not, even incipiently, display any of the specializations of myohyracines or mylomysgalines. It does resemble both the Rhynchocyoninae and the Macroscelidinae, agreeing with one or the other now in this character, now in that, and differing from both of them in the long symphysis. Resemblances to *Rhynchocyon* — and differences from the macroscelidines — are the small size of the talonid of M_2 relative to the trigonid and the small size of M_2 as a whole relative to M_1 . *M. stromeri* resembles the Miocene *R. clarki* in that the crista obliqua runs only to the posterior face of the trigonid and not to the

apex of the metaconid, but this is interpretable simply as a primitive character possessed in common. Resemblances to the Macroscelidinae, or at least to some of them, are the lack of a posterior accessory cusp on P_3 , the small single-rooted P_1 , the closely appressed roots of P_2 , the median position of the paraconid in the molars, the lingual groove of the incisor, and the steeply rising ascending ramus. In sum, the characters suggest relationship with the macroscelidines rather than with the rhynchoeyonines, and I very tentatively place *Metoldobotes* in the Macroscelidinae.

PALAEOTHENTOIDES Stromer

Palaeothentoides Stromer, 1932, p. 185.

Type species: *P. africanus* Stromer, 1932.

Distribution: Early Pleistocene?, southwest Africa.

Emended diagnosis: Lower postcanine formula P_4, M_3 ; P_1 two-rooted, not incisiform; P_{2-3} with anterior cusps little separated from protoconids, P_3 without metaconid and entoconid rudiments; P_4 narrow, metaconid decidedly posterointernal to protoconid, reëntrant valley between metaconid and entoconid nearly filled by swelling on crest running anteroexternally from entoconid, paraconid crest high, anterointernal swelling partially obliterating cleft between anterior crest and metaconid; M_{1-2} with very slight, shallow clefts between paraconids and metaconids, sides of deep reëntrants between metaconids and entoconids parallel, not ventrally converging; horizontal ramus of nearly even depth beneath cheek teeth, slightly downcurving anteriorly.

PALAEOTHENTOIDES AFRICANUS Stromer

(Fig. 2; Pl. 1)

Palaeothentoides africanus Stromer, 1932, pp. 178-185, figs. 1a-2b; Butler and Hopwood, 1957, p. 11.

Type: München No. 1931. VII. 1a, left ramus with $P_3 - M_2$, alveoli for P_{1-2}, M_3 .

Hypodigm: Type, and München Nos. 1931. VII. 1b, fragment of left ramus with M_{2-3} (now lost), and 1932. I. 501, left ramus with $P_1 - M_3$.

Horizon: The "intermediate terrace" of Wagner and Merensky (1929, p. 29, fig. 5); age uncertain, possibly early Pleistocene. Stromer (1931, p. 41; 1932, p. 185) considered this to be "wohl Mittelpliocän," which would now, with the transfer of the Villafranchian to the Pleistocene, be regarded as late Pliocene. The two other forms definitely identified by Stromer from this level,

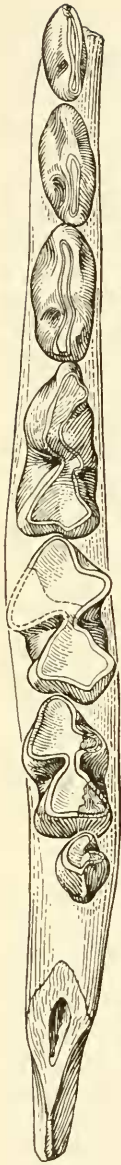
Enhydriodon and *Hyaena* (especially the latter), are not inconsistent with a Pleistocene age.

Locality: Klein Zee (or Kleinsee), near the mouth of the Buffels River on the coast of Little Namaqualand, some 25 miles SSE of Port Nolloth, Union of South Africa.

Diagnosis: As for the genus. Comparable in size to the smaller living macroscelidines.

Description: The first premolar is a long, narrow, double-rooted tooth with a simple crown consisting of a procumbent protoconid, which extends forward beyond the anterior root, connected by a crest to a smaller posterior cusp. The lingual face of the tooth is very slightly convex, the labial vertically grooved between the cusps. P_2 bears a small cusp on the anterior slope of the erect protoconid; labial and lingual grooves are present anterior to the protoconid, and the labial groove between protoconid and posterior cusp is much larger and deeper than in P_1 . All these features are accentuated in P_3 : the anterior cusp is larger, the grooves deeper, and the posterior cusp larger and wider; there is no metaconid or entoconid rudiment. These three teeth progressively increase in length and height. P_{1-3} of *Palaeothentoides* are very similar to the corresponding teeth of *Nasilio*, differing from those of the other living genera in various particulars. Thus, in *Macroscelides*, P_1 is single-rooted and similar in structure to $I_2 - C$, while P_{2-3} are higher crowned relative to length; in *Elephantulus*, P_1 has a higher protoconid, P_{2-3} have the anterior cusps well separated from the protoconid, P_3 has metaconid and entoconid rudiments, and a rudiment of the metaconid is occasionally seen on P_2 ; in *Petrodromus* and *Rhynchocyon*, all three teeth are higher, more piercing (especially the caniniform P_1 of the latter), anterior cusps are either lacking entirely (*Rhynchocyon*) or rudimentary (*Petrodromus*), while the posterior cusps are very small in both and, in *Rhynchocyon*, confined to P_3 .

P_4 , the longest of the cheek teeth, is submolariform, the talonid completely as in M_{1-2} , the narrow trigonid not. The entoconid is fully as large as in the molars and, as in them, higher than the hypoconid. In the trigonid, the anterior cusp is set off labially from the protoconid by a vertical groove wider and shallower than the corresponding ones on the anterior premolars. The groove between these two cusps on the lingual side is shallow and partially filled by a buttress on the side of the ridge connecting them. The metaconid is well developed, nearly as high as the protoconid and decidedly posteriointernal to it in position; the short crest between the cusps bears a small, shallow groove on its lingual side. The



crista obliqua runs to the apex of the metaconid. The labial reentrant between trigonid and talonid is fully as large and deep as in M_{1-2} , but the lingual is to a great extent filled by a vertical swelling on the side of the ridge running from the entoconid to the crista obliqua. The sides of this lingual reentrant are nearly parallel for most of their heights and converge to form a U only near the base of the enamel. The tooth continues the progressive increase in crown height seen in P_{1-3} . Although thoroughly macroselidid in structure, P_4 is the most distinctive tooth of the series. None of the living forms has the labial reentrant between trigonid and talonid nearly filled by a swelling, and in none is the metaconid so far posteriointernal to the protoconid. In all except *Macroselides* the anterior crest and the metaconid are widely separated by a deep groove and the sides of the lingual reentrant converge toward the base, forming a V.

M_{1-2} consist essentially of two triangular prismatic columns connected by the narrow isthmus formed by the crista obliqua. The protoconids, hypoconids and paraconids are angulate, the metaconids and entoconids more rounded. The paraconids and metaconids are separated by very shallow vertical grooves. The lingual and labial reentrants are large, deep, and extend nearly to the base of the enamel; their sides are parallel and U-shaped below. The trigonids are wider and larger than the talonids, particularly on M_1 . The metaconids and entoconids are higher than the protoconids and hypoconids, and there is a slight indication of a hypoconulid. This cusp may have been larger on the unworn crown, if we may judge from *Macroselides* in which it is very prominent on unerupted molars but rapidly becomes worn away. On the lingual sides of the crests running forward from the entoconids are faint vertical swellings corresponding to the

Figure 2. *Palaeothentoides africanus*, dorsal view of mandible, München No. 1932. I. 501. $\times 8$.

prominent one in P_4 . These molars are the highest crowned of the cheek tooth series. M_3 is vestigial and much lower crowned than M_2 . It is composed of the trigonid only, on which the small metaconid is the highest element and the protoconid is subordinated in the paraconid crest; metaconid and paraconid are separated lingually by a shallow depression, and there is a slight vertical ridge on the posterior face, the last vestige of the talonid. The enamel is continuous on all cheek teeth; it is thick on $P_4 - M_2$ although thinning at the paraconids in the molars. M_3 is indistinguishable from that of *Nasilio*. M_{1-2} , on the contrary, are quite different from those of this form and very close indeed to those of *Macrosclides*, differing only in their slightly lower crowns and, at a corresponding stage of wear, in the presence of enamel around the paraconids. In the other living forms, M_{1-2} are somewhat lower crowned, have wide lingual grooves between the paraconids and metaconids, and V-shaped sides to the lingual reentrants separating trigonids and talonids.

Seen from above, the ramus curves very slightly inward from P_2 forward and gently outward from M_3 backward. There is no trace of the symphysis on the part preserved, indicating that, as in all living macrosclidids except *Petrodromus*, this did not extend posteriorly beyond the level of the canines. The inner face, as noted by Stromer, is nearly flat, the outer swells out gently opposite the molars. As in other forms, there is a posterior mental foramen beneath P_4 and an anterior beneath P_1 . The height of the horizontal ramus remains rather constant beneath the cheek teeth, decreasing less anteriorly than in the living forms. The ventral border is gently convex beneath the molars and P_4 , and shows a more marked tendency to turn down beneath P_{1-2} than in any other form. As is usual in the group, the ascending ramus begins to rise well behind the last molar and the masseteric fossa is shallow and poorly defined.

Discussion: *Palaeothentoides* is unquestionably a valid genus. It resembles *Nasilio* and *Macrosclides*, combining characters of both, and can be referred with assurance to the Macrosclidinae. There is no need to belabor the fact that this form is no marsupial. A resemblance does exist, particularly in the trigonid, between P_4 of *Palaeothentoides* and M_1 of *Palaeothentes*, but this is far from exact. The labial and lingual reentrants separating trigonid and talonid that are large and deep in the African form are, for example, shallow in the South American one, and in any event the teeth Stromer compared are not homologous.

Stromer himself realized almost at once that *Palaeothentoides* was not a marsupial. A separate of his paper in my possession bears a typewritten slip reading: "*Berichtigung*: Durch einen neuen Fund ist erwiesen, dass *Palaeothentoides* 4 Pm and 3 M hat, also sicher kein Didelphier ist." So far as I am aware, however, he never published this retraction. The "new find" referred to is of course No. 1932. I. 501, here described and figured for the first time.

Measurements, in mm, of München No. 1932. I. 501.

	P ₁	P ₂	P ₃	P ₄	M ₁	M ₂	M ₃
Length	1.4	2.0	2.3	2.8	2.4	2.1	0.8
Width	0.6	0.7	0.9	1.4	1.7	1.5	0.8
Length P ₁ - M ₃ , 14.0; P ₁₋₄ , 8.6; M ₁₋₃ , 5.6.							
Height of ramus beneath M ₁ , external, 2.9.							

ELEPHANTULUS Thomas and Schwann

Elephantulus Thomas and Schwann, 1906, p. 577.

Elephantomys Broom, 1937, p. 758.

In the course of describing the Pleistocene *E. langi*, Broom observed that certain species of the genus, *langi* among them, have a molariform P². Believing that *E. rupestris*, the type species, lacked this character, he proposed *Elephantomys*, with *E. langi* as type, for the reception of those species possessing it. Shortly thereafter, specimens from what he supposed to be the type locality of *E. rupestris* having come to hand, he concluded that this species did after all have a molariform P², a fact which in his opinion effectively suppressed *Elephantomys*. He did not go on to erect a new genus for those forms with a non-molariform P².

Elephantomys was subsequently revived by Ellerman, Morrison-Scott and Hayman (1953, p. 8). Stating that P² of the type of *E. rupestris* was non-molariform, they recognized *Elephantomys* as a subgenus, distinguishing it on the basis of the molariform P² and the possession of less flattened bullae, in which the lateral (i.e. tympanic) portion is higher relative to the median (i.e. entotympanic) than in *Elephantulus*¹. These distinctions are not valid. As regards P², what is involved is a forward extension of the molarisation field. In *Rhynchocyon* and *Petrodromus* this extends hardly or not at all beyond P⁴; in *Nasilio* and *Macroscelides* P²⁻³ have been incorporated to the degree that two lingual cusps are

¹ They also reduced *Nasilio* to the rank of a subgenus of *Elephantulus*. This does not seem justified. In addition to possessing M₃, *Nasilio* has higher-crowned posterior cheek teeth and different hind limb proportions (Evans, 1942).

present on them. *Elephantulus* is in a state of flux. Among the material available to me, P² is molariform in *intufi* (5 specimens) and *fuscipes* (2), non-molariform in *rupestris* (5) and *pulcher* (7). Although predominantly non-molariform in *ocularis* (29) and *rufescens* (6), it is nevertheless variable in these species, even within what are surely local populations. Thus, in *rufescens* from Mt. Mbololo, Kenya, of two specimens collected on the same day, one (MCZ 31800) has two lingual cusps on P², another (MCZ 31802) one. Within *ocularis*, a small series from Unyanganyi, Tanganyika, Tanzania, includes two specimens (MCZ 25660 and 25683) with two lingual cusps on this tooth and three with one; a specimen from Dodoma, Tanganyika (MCZ 22841), has two lingual cusps on the left side and one on the right. Within the "non-molariform" species, P³ as well as P² is variable in respect of lingual cusp development. A distinction based on bulla structure cuts across one based on premolar structure. Thus the "non-molariform" *pulcher* has a "flattened" bulla, and the predominantly "non-molariform" *rufescens* and *ocularis* have "less flattened" ones. *Elephantomys* does not merit recognition.

A far reaching proposal for a division of *Elephantulus*, and indeed of the whole subfamily, has been advocated by Van der Horst, who, with co-workers, devoted many years to study of the embryology of the genus, with particular reference to *E. myurus jamesoni* (I employ Van der Horst's names in this paragraph). In the course of his work there emerged the remarkable facts that in this form approximately sixty eggs are liberated and approximately sixty corpora lutea develop in each ovary, only one of which becomes implanted, the Graafian follicle is remarkably small, and fat globules are lacking in the ova. *Macroscelides proboscideus* was found to agree in all these particulars, and *E. capensis* in all save for the presence of a few fat globules. *E. intufi* and *E. rupestris* stand in striking contrast. In these species only two eggs per ovary are liberated, the Graafian follicle is of normal type, and fat globules are present. *Petrodromus tetradactylus* is in agreement with them except for the apparent absence of fat globules. On the basis of all this, Van der Horst has suggested (e.g. 1944) that there are only two genera of macroscelidines and that the division passes through the genus *Elephantulus* of current usage. He has not spelled out what would result were his suggestion to be adopted, but this can be simply put. We would have two genera: *Macroscelides*, with *proboscideus*, *myurus* and *capensis*, and *Petrodromus*, with *tetradactylus*, *rupestris* and *intufi*; all other species would have to remain in limbo until comparable investigations had been

carried out on them. If these characters were indeed the touchstone of macroscelidine systematics such a situation would be acceptable, but there is no real evidence that they are. The genera recognized by mammalogists over the years are clear-cut taxa, distinguishable by different combinations of characters. The sporadic occurrence of the curious ovarian characters suggests that these were independently acquired, or, alternatively, perhaps lost, at various times within the group.

This possibility is reinforced if the classification, other than subgeneric, of the South African species and subspecies of *Elephantulus* proposed by Ellerman, Morrison-Scott and Hayman is correct. Van der Horst's *myurus jamesoni* is their *rupestris jamesoni*, his *capensis* is their *rupestris capensis*, his *intufi* and *rupestris* may be their *rupestris* and *intufi*. His division of the subfamily would thus run between subspecies of *rupestris* in their arrangement. The genetic basis of the ovarian peculiarities may be of a rather simple sort.

ELEPHANTULUS LANGI (Broom)

Elephantomys langi Broom, 1937, pp. 758-760, fig. 5.

Elephantulus langi Broom, 1938, p. 251; 1948, p. 5.

Horizon: Pleistocene.

Locality: Cave deposit at Schurveberg, 15 miles west of Pretoria, Transvaal, Union of South Africa.

E. langi is evidently represented by rather rich material from the Schurveberg cave deposit, and Broom's description is of the most preliminary sort. The relationship between *langi* and living forms remains to be determined.

ELEPHANTULUS ANTIQVUS Broom

Elephantulus antiquus Broom, 1948, pp. 5-6, fig. 3.

Horizon: Earlier Pleistocene.

Locality: Bolt's workings, Sterkfontein, Transvaal, Union of South Africa.

E. antiquus is evidently distinct from *E. langi*—it has, e.g., a non-molariform P²—but little more can be said. As in the case of *E. langi*, there is fairly abundant material, Broom's description is preliminary and incomplete, and the relationship to living species is unknown. In 1946, Broom (*in* Broom and Schepers, p. 78) stated that: "The elephant shrew *Elephantulus langi*, or one very closely allied, occurs in the Plesianthropus cave. The type is from Schurveberg, Pretoria. It is common at Bolt's workings." Presumably the species there referred to is *E. antiquus*.

ELEPHANTULUS ROZETI (Duvernoy)

From an archaeological site at Redeyef, Tunisia, Gobert (1912) recorded the presence of various genera of mammals, most of which he believed to be referable to living species. *Macroscelides* (*sic*) is among those listed. Three cultural levels occur at the site, the two lower Paleolithic and the upper ranging from transitional to Neolithic. Gobert gave no description of the mammalian remains, which it would appear from the text were found in the upper level. Romer (1928, pp. 100, 153, 161) lists this find as *Macroscelides rozeti*. A little uncertainty attaches to the determination. Thomas (1901, 1913) split North African *Elephantulus* into two species, *E. rozeti* and *E. deserti*, the former with three and the latter with two subspecies. *E. deserti* is the more eastern of the two and, if valid, the Redeyef material might therefore be referable to it. More likely than not, however, subspecific distinction, at most, is involved. Although Thomas had stated, in 1901, that *deserti* did not differ in size from *rozeti*, he claimed, in 1913, that it was smaller; the very few published measurements do not support the assertion. The differences appear to be confined to pelage color.

Elephantulus rozeti, which dates from 1838, was long known as *Macroscelides rozeti*, and numerous specimens so labeled found their way into collections. Many of the labels were not changed when Thomas and Schwann transferred *rozeti* to their new genus *Elephantulus*. These labels have trapped trusting anatomists and paleontologists. A number of accounts and illustrations in the literature that purport to be of *Macroscelides* are actually of *Elephantulus*, based on *E. rozeti* (e.g. Evans 1942, Fiedler 1953, Grassé 1955, Saban 1956-1957, Van der Klaauw 1929, in part).

RHYNCHOCYONINAE

RHYNCHOCYON Peters

RHYNCHOCYON CLARKI Butler and Hopwood

R. clarki Butler and Hopwood, 1957, pp. 4-11, figs. 2-3.

Horizon: Early Miocene.

Localities: Type from Songhor local fauna, Kenya; referred material from Rusinga Island, Kenya, found in the upper and lower Hiwegi beds and either in the Kiahera or in the lower part of the Kathwanga beds.

This species, so well described by its authors, reveals, as they point out, that the two surviving subfamilies had diverged prior to

the Miocene. *R. clarki* ". . . as an early member of the *Rhynchocyon* lineage . . . is . . . nearer to the common ancestor of the two groups, and possesses a number of primitive characters which have been lost in Recent representatives of both subfamilies." The species is notably smaller than the living members of the genus, which suggests a relatively recent increase in size within the *Rhynchocyon* lineage.

MYLOMYGALINAE subfam. nov.

Diagnosis: I₃, C, P₄, M₂. I₁₋₃ small, subequal; C — P₂ small, single rooted; P₄ — M₂ large, hypsodont, crowns complex, flat, of grinding type. Molars compressed anteroposteriorly, as wide as long; protoconid and hypoconid angulate, directed antero-externally; hypoconid and hypoconulid forming posterior lophid, entoconid set off from posterior lophid by deep reëntrant; reëntrant between paraconid and metaconid situated on anterior face of tooth; M₂ large relative to M₁. Talonid of P₄ fully molari-form, trigonid larger, more elongate than in molars. Ventral border of horizontal ramus strongly convex, alveolar border concave beneath posterior cheek teeth.

MYLOMYGALE Broom

Mylomygale Broom, 1948, p. 6.

Type species: *M. spiersi* Broom.

Distribution: Earlier Pleistocene, south Africa.

Diagnosis: Sole known genus of the subfamily diagnosed above.

MYLOMYGALE SPIERSI Broom

(Fig. 3)

Mylomygale spiersi Broom, 1948, pp. 6-8, fig. 4, (1946, *in* Broom and Schepers, p. 28, fig. 1 N-O¹).

Locality: ". . . a small cave about half a mile to the north of the cave which yielded the Taungs man-ape skull." Approximately 80 miles N. of Kimberly, Bechuanaland, Union of South Africa.

Horizon: Earlier Pleistocene. ("This bone breccia is probably of approximately the same age as [those in] the other caves.")

Diagnosis: Sole known species of the genus.

Discussion: This remarkable little macroselidid enjoys the distinction of being the only extinct genus correctly placed in the

¹ In this paper *M. spiersi* was figured and listed with the statement that: "It represents a new family of the Menotyphla." No diagnosis or description was given.

family by its describer. Discovery of *Mylomysgale* revealed the existence of an otherwise unknown division of the family, one that evolved posterior cheek teeth that are as strikingly rodent-like as those of the myohyrcines are ungulate-like. Broom's remark to the effect that had the molars been found isolated they would have been regarded as belonging to some peculiar hystricomorph rodent is no exaggeration.

The type specimen preserves five small alveoli followed by four grinding teeth. Although he decided that the dental formula was probably I_3, C, P_4, M_2 , Broom was in some doubt as to whether the last two alveoli housed the roots of two teeth or of one. "As in all the living *Macroscelids* the anterior premolars are double-rooted it might seem more probable that the two sockets held a single premolar, but on the other hand if the anterior premolar were double-rooted then there can only be three premolars, while all living *Macroscelids* have four. . . . I think it more likely that there were two small single-rooted premolars." This tentative conclusion was, I believe, the correct one. Contrary to Broom's statement, and as pointed out above, the roots of P_1 are fused in *Macroscelides*, in some species of *Elephantulus*, and in the extinct *Metoldobotes*, while the roots of P_2 are closely appressed in *Macroscelides*. The anterior portion of the horizontal ramus is short in *Mylomysgale*, and it is hence not surprising that the roots of P_2 had fused.

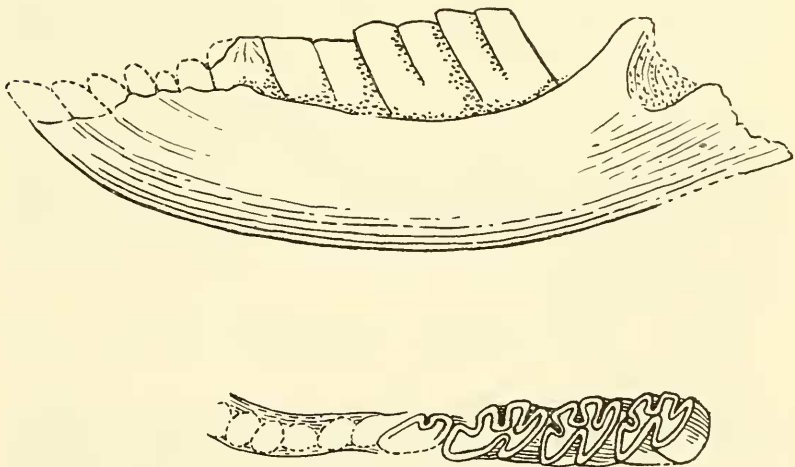


Figure 3. *Mylomysgale spiersi*, lateral view of mandible and crown view of dentition, $\times 4$; redrawn from Broom.

P_3 , the most anterior tooth preserved, bears the same size relation to P_4 , and P_4 to the molars, as in other members of the family. P_4 and the two molars are remarkable for their deep, narrow, and persistent reëntrant folds. Comparison with an unworn molar of *Macroscelides* (Fig. 5h) permits an understanding of the cusp pattern. The anteroexternal angle is composed of the protoconid and the centrally situated paraconid. Hypoconid and hypoconulid are joined to form the posteroexternal and posterointernal angles and the posterior lophid. The metaconid makes up the antero-internal angle and the entoconid the central internal. This degree of independence of the entoconid is a departure from the usual macroscelidid condition, in which entoconid and hypoconulid tend to be connected (cf. Fig. 1a, b). The large size of M_2 relative to M_1 is another character peculiar to *Mylomysgale* within the family; in all other known genera, even in the earliest, *Metoldobotes*, it is decidedly smaller than its predecessor in the series. The size of this tooth provides an example of the reversal of an evolutionary trend, the reversal in this case being associated with the later trend toward the acquisition of rodent-like posterior cheek teeth.

MYOHYRACINAE

(= Myohyracidae Andrews 1914, Myohyracoidea Stromer 1926)

(Figs. 4b; 5a, b, c, f, i, j; 6a, c, e, g, i)

Emended diagnosis: Macroscelididae with complete dental formula; 1_{1-2}^{1-2} large, without enamel on lingual faces; posterior cheek teeth hypsodont; M_3^3 greatly reduced; P_2^{2-3} submolariform, P_4^4 essentially molariform; $P^3 - M^2$ with moderately undulant ectoloph, paracones and metacones with comparatively shallow labial grooves between them, parastyles and metastyles prominent, parastyles anteroexternal in $P^4 - M^2$; $P^2 - M^2$ with persisting fossettes, those of molars arranged in anterior and posterior pairs; $P_3 - M_2$ with two fossettids, one each in trigonid and talonid; horizontal ramus deep beneath posterior cheek teeth, mental foramen beneath P_3 .

Distribution: Early Miocene, east and southwest Africa.

Genera included: *Myohyrax* Andrews 1914, *Protypotheroides* Stromer 1922.

Discussion: Andrews (1914, pp. 169-171) described *Myohyrax oswaldi* on a fragment of a ramus with $P_3 - M_2$ and some isolated teeth, including an upper molar; this material gave no hint of the vestigial nature of M_3^3 . With such evidence in hand it would hardly occur to anyone to make a comparison with the macroscelidids, and Andrews did not do so. He referred the genus to a

new family of the Hyracoidea. All subsequent students have looked at myohyracines in this light and some of them have commented on how aberrant they are within that order. From the work of Stromer (1926) and of Whitworth (1954), it is possible to note that many of the characters in which they differ widely from hyracoids are actually points of resemblance to macroscelidids.

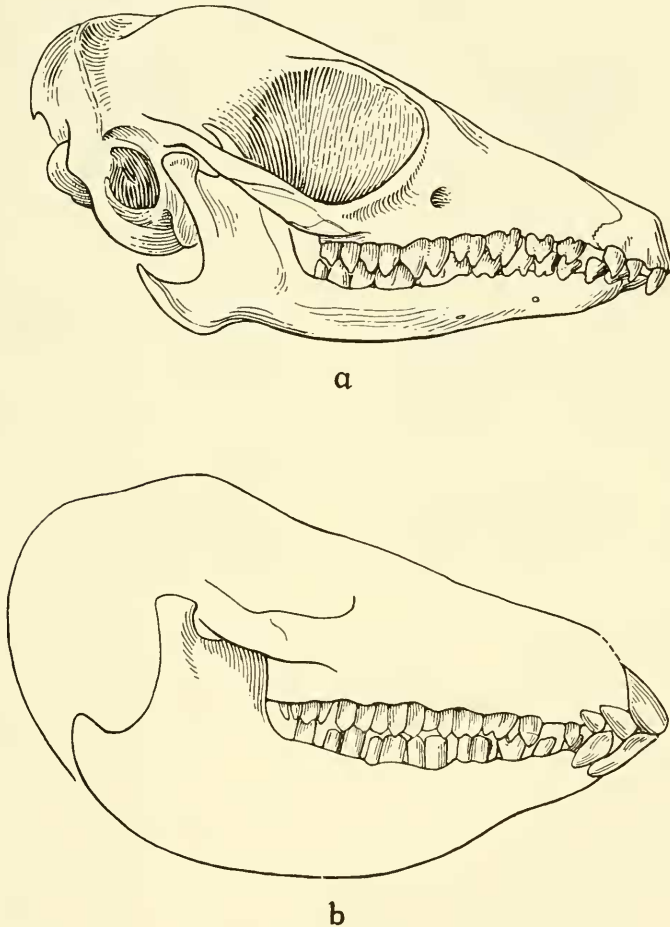


Figure 4. Lateral views of skull and mandible of, *a*, *Nasilio brachyrhynchus*, MCZ 43755, and, *b*, *Myohyrax oswaldi*, slightly modified from Whitworth; *b* $\times 2$, *a* not to scale.

The skull of *Myohyrax*, figured in outline by Whitworth, is not dissimilar to those of other members of the family (Fig. 4). The facial region in all is long, low and rather narrow; the cranium is short and high; the zygoma arises over the rear of M^1 ; and the glenoid cavity is situated high on the side of the skull. Whitworth shows a slight notch between nasal and premaxilla; I was unable to detect this in the specimen. The palate is unfortunately not visible. The myohyracine mandible, if allowance be made for the increased depth beneath the hypsodont cheek teeth, is decidedly macroscelidid in appearance. The symphysis is short and shallow; the ascending ramus high and steeply rising, and the coronoid process small; the condyle is high and not expanded transversely; and the angle is hook-like and extended posterodorsally.

$P^2 - M^2$ of *Macroscelides* and *Nasilio* resemble the corresponding teeth of *Myohyrax* in a number of respects. The posterior cheek teeth of myohyracines are somewhat bowed outwardly (Whitworth, 1954, pl. 6, fig. 2), $P^2 - M^1$ are inclined backward and $P_3 - M_2$ are inclined forward; the bowing is incipient and the pitching definitely present in *Macroscelides*. M^2 of myohyracines is unreduced, in correlation with the retention of M_3^3 ; in *Nasilio*, in which M_3 is retained, the posterior portion of M^2 is less reduced than in the other living forms. The great reduction of M_3^3 is, of course, a decided resemblance to the macroscelidids and a striking contrast to the hyracoids. The crown pattern of the upper molars of the myohyracines (Fig. 5) is basically macroscelidid and not hyracoid in such characters as the large, external paracone and metacone, the absence of a mesostyle (in this I agree with Andrews and with Hopwood, believing Whitworth's mesostyle to be the paracone), and the position and relations of the lophs. In macroscelidines, especially *Macroscelides* and *Nasilio*, the lophs are relatively high, the protoloph going to the parastyle, the robust metaloph primarily to the paracone; the protocone is connected posteroexternally to the enlarged anteroexternal portion of the metaloph and the posteroloph is transverse, connecting metastyle and hypocone, all very much as in myohyracines. Between paracone, protoloph, metaloph and protocone anteriorly, and between metacone, metaloph and posteroloph posteriorly, two fossettes are isolated. These are aligned anteroexternally to posterointernally, and are the homologues of the anterior and posterior pairs of fossettes in the upper molars of myohyracines. In unerupted or little worn molars of *Macroscelides* tendencies toward division of each of these fossettes into two may be seen.

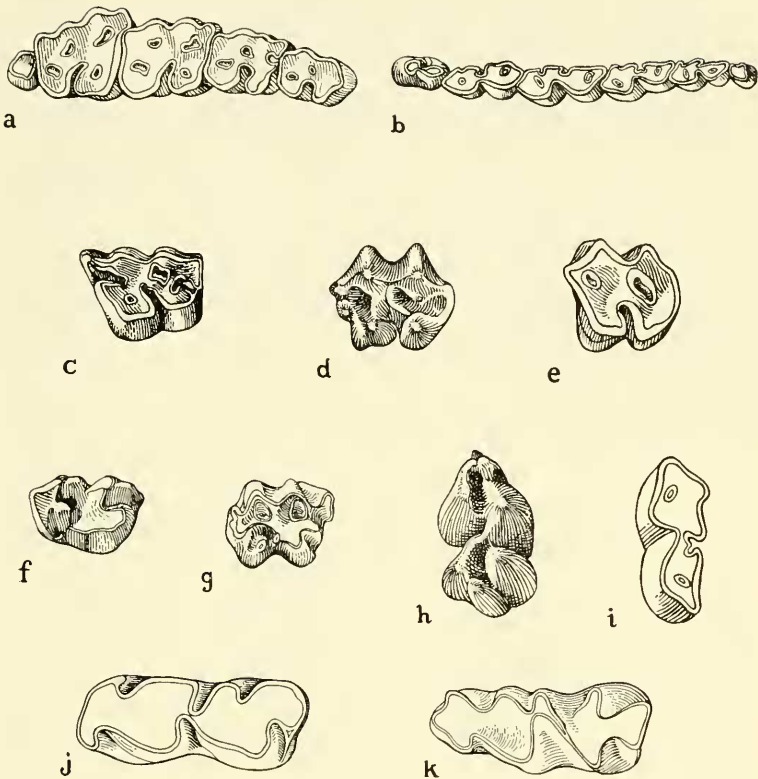


Figure 5. A comparison of myohyracine and macroscelidine cheek teeth. *Myohyrax oswaldi*: a, P³ - M³; c, M²; f, dm⁴; j, dm₄. *Protypotheroides beetzi*: b, P₂ - M₃; i, M₁. *Macrosclides proboscideus*: d, M¹ (unworn); e, M¹; g, dm⁴; h, M₁ (unworn); k, dm₄. a, b, c, f, i redrawn from Stromer, j from Whitworth; d, g, h, k MCZ 37022, e MCZ 37023. b × 2; a, c, f, i × 4; j × 6.6; the rest not to scale.

The crown structure of P₄ and of the lower molars is close to that of *Palaeothentoides* and *Macrosclides* (Fig. 5). The lingual re-entrant between trigonid and talonid is less open than in these forms, and this narrowing was probably brought about by a swelling on the entoconid crest similar to but larger than that present in *Palaeothentoides*. *Macrosclides* has fossettids in the trigonids and talonids of unworn molars and these are closely comparable, although much shallower than those occurring in *Protypotheroides*.

The fourth upper milk molar of *Myohyrax* (Fig. 5f), like the permanent molars, is very similar to the corresponding tooth in macroscelidines. The differences that exist between it and that of, e.g., *Macroscelides* — parastyle less set off by grooves, more prominent posteroloph, nearly straight lingual wall, protocone not set off by an anterior groove — do not disguise the basic resemblance. Dm_4 of *Myohyrax* (Fig. 5j), although considerably worn, is again unmistakably macroscelidid in structure and quite unlike that of hyracoids. As in all members of the family, it is very long and low-crowned, with trigonid and talonid approximately equal in length. The paraconid area is set off by external and internal grooves from the large protoconid and the even larger metaconid, which was almost certainly twinned as it is in *Macroscelides*. The paraconid was clearly anterocentral in position with a short labial crest and a longer lingual one terminating in a parastylid. Lingual and labial reentrants between trigonid and talonid are essentially as in *Macroscelides*. The hypoconid is very large; the entoconid and hypoconulid have become united by wear, while the groove between hypoconid and hypoconulid still persists. With wear this would occur in *Macroscelides*. An entostylid is present anterior to the entoconid, set off by grooves from it and from the metaconid; a precisely similar structure occurs in dm_4 of *Petrodromus*. I differ from Whitworth as regards cusp homologies in this tooth. My parastylid is his paraconid, my entoconid and hypoconulid are regarded by him as a styler development and my entostylid is his entoconid. In hyracoids, dm_4 is somewhat narrower relative to length than is M^1 , which it otherwise resembles very closely, and dm_4 and M_1 are nearly identical.

Stromer (1926) described and figured various posteranial fragments, which he referred to *Myohyrax*. Except for an atlas, which may not be correctly identified, all of these are decidedly macroscelidid in appearance. Figure 6 shows a selection of these fragments, redrawn from Stromer, compared with corresponding parts of a living member of the family. The resemblances are obvious and do not need to be elaborated. One point may be stressed. The astragalus is about as different as possible from that of hyracoids. This element in the latter is as distinctive in its way as are the corresponding bones of artiodactyls and perissodactyls. In the hyracoid astragalus the articular area of the trochlea continues distally over the medial side of the short neck into a curious, step-like surface for the reception of the long, stout internal malleolus of the tibia. This specialization had already been attained by early Oligocene, Fayum forms, the earliest known

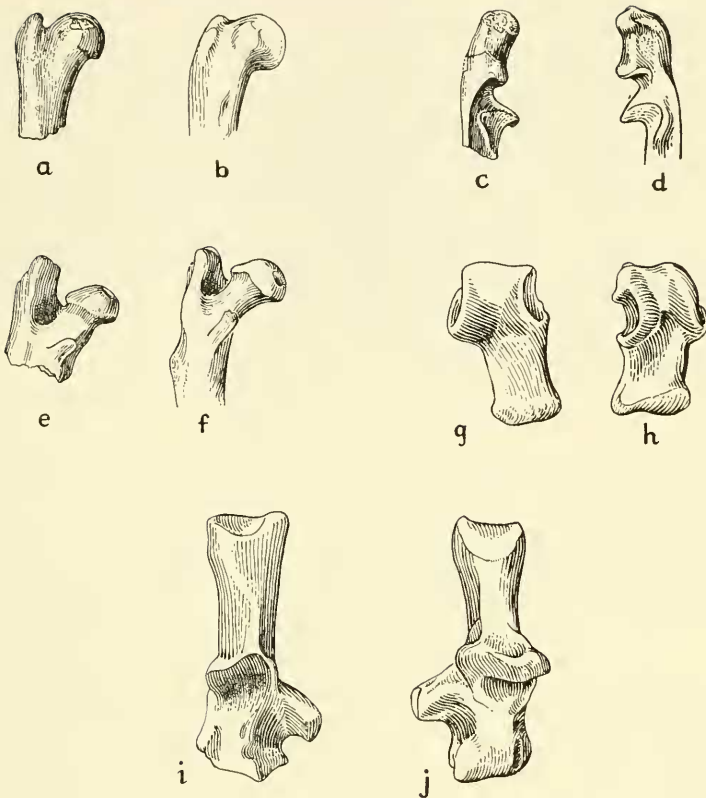


Figure 6. A comparison of myohyracine and rynchocyzone postcranial elements. *Myohyrax oswaldi*: a, c, e, g, i; *Rynchocyzone cirnei*: b, d, f, h, j. a, b, proximal ends of humeri; c, d, proximal ends of ulnae; e, f, proximal ends of femora; g, h, astragali; i, j, calcanea. a, c, e $\times 2$; g, i, $\times 4$; *R. cirnei* not to scale. *M. oswaldi* redrawn from Stromer, *R. cirnei* MCZ 43735.

members of the order (Schlosser, 1911, p. 126, pl. 13, fig. 2). The comparatively long-necked myohyracine astragalus shows no trace of such a structure, and agrees in all essentials with those of other macroscelidids (Fig. 6 g, h). It is regrettable that none of these pieces is complete enough to give any idea of the degree of fusion of the lower leg bones, not to mention the relative lengths of the limb segments or of the fore and hind limbs. Whether or not

the myohyracines were saltatorial, as are living forms¹, remains unknown.

Four species of early Miocene myohyracines have been described: *Myohyrax oswaldi* Andrews 1914, *Protypotheroides beetzi* Stromer 1922, *Myohyrax doederleini* Stromer 1926, and *Myohyrax osborni* Hopwood 1929. Of these, *M. oswaldi* and *M. doederleini* are small and very similar, *P. beetzi* and *M. osborni* are much larger and very similar. Whitworth recognizes but two species, *oswaldi* and *beetzi*, and in this he is undoubtedly correct. He goes on to synonymize *Protypotheroides* with *Myohyrax*, but here I am unable to follow him. It appears to me that the differences between the two valid species, summarized in the diagnoses below, are of generic significance, as genera are defined in this family.

MYOHRAX Andrews

Myohyrax Andrews, 1914, p. 171.

Type species: *M. oswaldi* Andrews, 1914.

Distribution: Early Miocene, east and southwest Africa.

Emended diagnosis: Myohyracines with cement in fossettes of cheek teeth; M³ single rooted; fossettids on P₃ — M₂ ephemeral.

MYOHRAX OSWALDI Andrews

Myohyrax oswaldi Andrews, 1914, pp. 169–171, pl. 28, figs. 4–6; Stromer, 1926, pp. 123–124, pl. 41, figs. 26–28; Whitworth, 1954, pp. 26–40, text-figs. 9–15, pl. 5, figs. 3–4, pl. 6.

Myohyrax doederleini Stromer, 1926, pp. 120–123, text-fig. 19, pl. 41, figs. 1–23; Hopwood, 1929, p. 6, text-fig. 4.

Horizon: Early Miocene.

Localities: Kenya: Koru (type locality), Karungu, and Rusinga Island (definitely recorded from the lower Hiwegi beds); South-West Africa: Elisabethfelder, a borehole some 37 km SSE of Lüderitzbucht (Stromer), and "south of Lüderitz Bay" (Hopwood).

Diagnosis: As for the genus. Intermediate in size between the species of *Petrodromus* and those of the smaller macroscelidine genera.

The combination of relatively persistent fossettes in the upper molars and ephemeral fossettids in the lower molars is almost precisely matched in *Macroscelides*. The species is common at

¹ It is sometimes stated (e.g. Evans, 1942, p. 85) on the basis of observations by field workers that, despite their evident saltatorial adaptations, macroscelidids do not hop but run on all four feet. Run they obviously do but hopping has also been observed.

certain localities. In South-West Africa, Stromer records over 100 from Elisabethfelder, and Whitworth (1958, p. 47) lists 120 from Karungu in Kenya.

PROTYPOTHEROIDES Stromer

Protypotheroides Stromer 1922, p. 333.

Type species: *P. beetzi* Stromer, 1922.

Distribution: Early Miocene, southwest Africa.

Emended diagnosis: Myohyracines without cement in fossettes of cheek teeth; M^3 two rooted; fossettids on $P_3 - M_2$ deep.

PROTYPOTHEROIDES BEETZI Stromer

Protypotheroides beetzi Stromer, 1922, p. 333; 1926, pp. 124-125, pl. 41, figs. 29-31.

Myohyrax osborni Hopwood, 1929, pp. 6-8, text-figs. 5-6.

Myohyrax beetzi Whitworth, 1954, p. 26.

Horizon: Early Miocene.

Localities: Langental, some 10 km NNE of Bogenfels (Stromer), and "south of Lüderitz Bay" (Hopwood), South-West Africa.

Diagnosis: As for the genus. A large species, for this family; comparable in size to *Rhynchocyon petersi* the largest living form.

Neither Stromer nor Hopwood mention cement in *P. beetzi*, and I was unable to detect any. The anterior wall of the alveolus of M^3 is preserved in the type of "*M. osborni*" and shows the presence of two roots. The fossettids extend nearly to the bases of the posterior cheek teeth. *P. beetzi* is rare in comparison with *M. oswaldi*, only eight specimens having been recorded.

DISCUSSION

INTRAFAMILIAL RELATIONSHIPS

Among the living forms, *Rhynchocyon* stands apart in a number of characters — e.g., largely or wholly edentulous premaxillae, upper canines large and P_1 caniniform, long and broad facial region, large cranial table, no palatal fenestrae, backwardly sloping ascending ramus, presence of chevron bones, radius and ulna not fused, digit I lacking and digit V reduced in the manus. The majority of authors agree in placing *Rhynchocyon* in a distinct subfamily and this seems justifiable. The extinct *R. clarki* shows that the subfamily was in existence by Miocene time, and in so doing provides us with the nearest approach to a phyletic lineage that we have. This species, as is not surprising, possesses some

macroscelidine characters; divergence of the two subfamilies may date from earlier Oligocene time.

The Macroscelidinae, with four living and two extinct genera, form the core of the family, so far as present knowledge goes. The various forms differ unevenly within rather narrow limits. The heights of the cheek teeth range from brachyodont in *Metoldobotes* and *Petrodromus* to subhypsodont in *Palaeothentoides*, *Nasilio* and *Macroscelides*, yet two of the higher crowned forms, *Palaeothentoides* and *Nasilio*, are primitive in their retention of a vestigial M_3 (*Metoldobotes*, the earliest known macroscelidid, had already lost this tooth). *Macroscelides* stands alone in its possession of highly inflated bullae and epitympanic sinuses. *Nasilio*, advanced as regards molar height, has the tibia shorter relative to the femur than in either *Elephantulus* or *Macroscelides* and resembles in this respect the rather generalized *Petrodromus*. The latter, in turn, is specialized as regards the loss of the hallux, and so on. *Palaeothentoides* and the living macroscelidines give the impression of being terminal twigs of a once more numerous and varied group. It is unsafe at present to assert that two or more members of the subfamily are closer to each other than to the rest phylogenetically, since characters in common could well have been achieved independently.

The two extinct groups, Myohyracinae and Mylomygalinae, best regarded for the present as subfamilies, are highly specialized as regards their cheek teeth, the former in an ungulate-like, the latter in a rodent-like direction. Unfortunately, we know them only at moments in time — the two myohyracines in the earlier Miocene, *Mylomygale* in the Pleistocene — and hence have no direct evidence bearing on their phylogenies. The myohyracines, which alone in the family retain M^3 as well as M_3 , may have branched off at an early date, possibly Eocene, the mylomygalines perhaps somewhat later. The ancestry of both groups may have lain in the Macroscelidinae, but this is uncertain.

The only extra-African form that has been referred to the family is *Pseudorhynchocyon cayluxi* Filhol (1892) from the Quercy Phosphorites. This very unsatisfactorily known animal was based on the posterior part of a left mandible, in which the alveoli of the last molar provide the only trace of the dentition. The ascending ramus is much inclined posteriorly, and Filhol saw in this a resemblance to *Rhynchocyon*. In fact, however, *Pseudorhynchocyon* in this respect goes far beyond conditions in the living form (Fig. 7). As Butler and Hopwood have pointed out, the ascending ramus of the Miocene *R. clarki* is considerably less inclined than in the

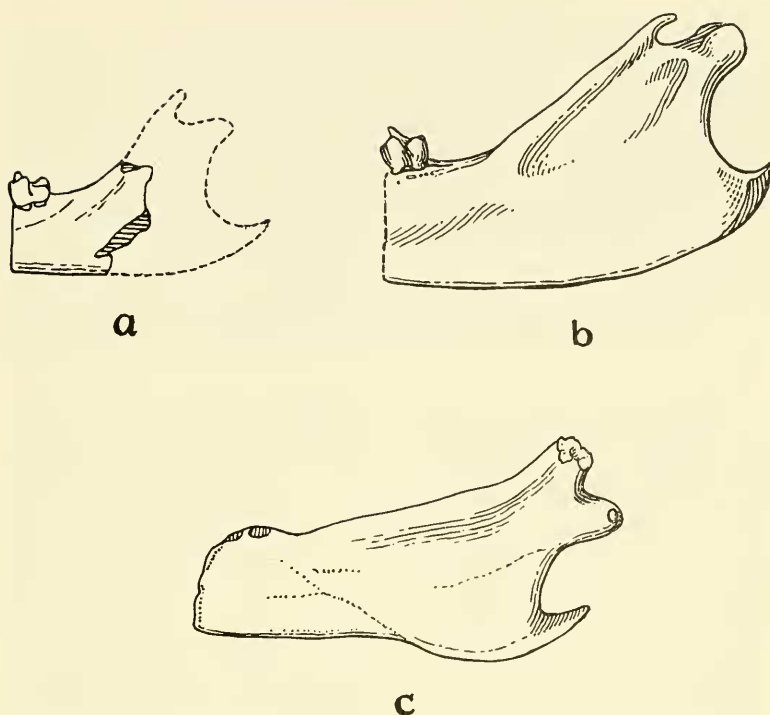


Figure 7. Posterior portions of mandibles of, *a*, *Rhynchocyon clarki*, *b*, *Rhynchocyon petersi*, *c*, *Pseudorhynchocyon cayluxi*. $\times 2$. *a* modified from Butler and Hopwood, *b* MCZ 22573, *c* redrawn from Filhol.

living species, which suggests that such inclination is of relatively recent acquisition within the subfamily. Besides this, there is nothing at all macroscelidid-like about the structure of the ascending ramus of *Pseudorhynchocyon*. The coronoid process is much stouter than in any member of the family and extends well above the condyle. The latter faces posteriorly and is level with the cheek teeth, not far above them. The angle is low, and a prominent masseteric crest leads downward and then upward from it, projecting down below the level of the ventral border of the horizontal ramus. Butler and Hopwood conclude that “. . . the reference of *Pseudorhynchocyon* to the Macroscelididae is most improbable.” They are quite right. Whatever the creature may be — and I can offer no constructive suggestion on this score — it is not a member of this wholly African family.

THE FOOD OF MACROSCOLIDIDS

The posterior cheek teeth of myohyracines are comparable as regards degree of hypsodonty and crown complexity to those of certain hypsodont notoungulates, or, in miniature, to those of late Miocene or early Pliocene Equinae. As both Hopwood and Whitworth emphasize, such specialization can only be regarded as an adaptation to a diet consisting in large part of harsh vegetation. *Myiomygale* has posterior cheek teeth that are similar in height and complexity to those of various hypsodont rodents. Within the Macroscelididae there have arisen two groups primarily adapted to an abrasive vegetable diet. It thus becomes important to ascertain if living members of the family are to some extent herbivorous.

Structurally, as has long been recognized, the macroscelidid jaw is basically that of a herbivore. The jaw muscles, especially *M. temporalis*, show resemblances to those of artiodactyls, although, as Fiedler (1953, p. 161) has pointed out, the disposition of the tendons (Sehnenskelet) is "insectivoran." The structure of the cheek teeth, particularly of the higher-crowned living forms, is consistent with a diet at least partially herbivorous. Is there evidence that these animals do in fact eat plants? Regrettably, no thorough study of the diet of any macroscelidid is available, and the anecdotal literature is unsatisfactory. Unsubstantiated assertions to the effect that macroscelidids are exclusively insectivorous are common. Reports by collectors that insects were found in stomachs are sometimes quoted, but insect remains are relatively easy to detect and would likely be looked for (macroscelidids being "insectivores"), whereas vegetable remains, if scanty, are more difficult to recognize and might even be passed over without comment on the supposition that they had been accidentally ingested together with the prey. Nevertheless, a few statements do suggest that these animals are omnivorous. Thus, Selater (1901, p. 155) states, on the authority of Francis, a collector, that *Petrodromus sultan* is ". . . very partial to the droppings of the Livingstone buck (*Nesotragus livingstonianus*).". Shortridge writes, of *Elephantulus* (1934, p. 21), ". . . although mainly insectivorous [they] are to some degree omnivorous, and may be caught in traps baited with mealies, quaker oats, etc."; and, of *E. intufi*, "examined stomach contents: insects and a small amount of vegetable matter" (p. 23). "The smaller species . . . feed mainly on ants . . . supplemented by tender shoots, roots and berries" (Walker *et al.* 1964, p. 134). The

most convincing statement is by Broom (1898, p. 68): "*Macroscelides*¹, the Elephant-shrew, has a jaw which judging by analogy would certainly be related to a herbivorous form and the molar teeth would seem to be quite in harmony with this determination, and yet though *Macroscelides* is largely a vegetable feeder [italics mine] I have found in the stomach abundant remains of ants and even of fairly large beetles." Although quite inadequate to reveal how large a role vegetable food may play in the macroscelidid diet, this small budget of information does reveal that plants in one form or another are eaten. If early members of the family were similarly omnivorous, the evolution of predominantly herbivorous phyla is readily understandable.

THE SYSTEMATIC POSITION OF THE MACROSCELIDIDAE

Real knowledge of the macroscelidids dates from 1829², when *Macroscelides* was described by Smith, and of the tupaiids from 1821², when Raffles proposed *Tupaia*. Neither group formed part of Bowdich's Insectivora of 1821, based on Cuvier's "les insectivores" of 1817, which included representatives of a majority of the living families. Given the knowledge available in the earlier part of the 19th century, however, it was inevitable that both families would be placed in this order. As knowledge improved it was equally inevitable that differences between them and the rest of the Insectivora would become increasingly apparent. Peters (1864), recognizing this, divided the order Insectivora into two major, unnamed groups, one with, one without a caecum, and included the colugos with the tupaiids and macroscelidids in the first. Haeckel (1866, p. cix), excluding the colugos, gave to these groups the formal names Menotyphla and Lipotyphla, the former based equally on the Cladobatida (= Tupaiidae) and the Macroscelidea (= Macroscelididae)³, the latter including the original Insectivora.⁴ With this, a stage was set. Elephant shrews and tree shrews became firmly associated in the minds of many investigators, and discussions of affinities, particularly of the former group, fell into a

¹ The old inclusive genus *Macroscelides* had not been subdivided at this date, and the question therefore arises as to whether Broom was dealing with the genus as now restricted. It is known, however, that in 1897-98 he resided in Little Namaqualand and hence was within the range of *M. proboscideus*.

² *Macroscelides* had been known since 1800, but disguised as *Sorex proboscideus*, *Tupaia* since 1820, but disguised as *Sorex glis*.

³ Simpson (1931, p. 16n; 1945, pp. 176, 183) has stated that Menotyphla was based on the macroscelidids; this does not appear to be the case.

⁴ There is some tendency nowadays to employ Lipotyphla as an ordinal name for the Insectivora minus the "Menotyphla." It needs to be emphasized, as McKenna (1963b, p. 4n) has done, that "Lipotyphla" is to all intents and purposes strictly synonymous with Bowdich's Insectivora.

rut. The characters the two families had in common were hailed as proof of close relationship, almost as though the possession of such things as caeca and normal mammalian zygomatic arches and pubic symphyses were peculiar to them. Even after attention had become focused on the evident resemblances to primates shown by the tree shrews and strong doubts had been cast on the reality of Haeckel's Menotyphla, some students continued to associate the two families closely, and even to waft the macroscelidids to the primate heights as a kind of ill-fitting tail to the tupaiid kite.

Inclusion of the Tupaiidae in the Primates is a view becoming more and more widely accepted. There is no occasion here to trace the development of this concept (Carlsson, 1909, 1922; Gregory, 1910; Le Gros Clark, 1934; Simpson, 1935, 1945; and others) or to review the imposing body of data that favors it. Some items of evidence that have not yet passed into the general literature may be mentioned, however. Henckel (1928) and Roux (1947) concluded that the chondrocranium of *Tupaia* excluded the family from the order Primates. This opinion was largely based on the absence of a septum interorbitale, a supposed hall mark of primates. Grassé (1955, p. 1649), who recognized Menotyphla in the Haeckelian sense, utilized this to offset Saban's (1956-7) conclusion, based on a thoroughgoing study of the adult skull, that tupaiids were members of the order. Recently, Starck (1960, 1962), working on a wide variety of primates, has found the septum interorbitale to be a highly plastic structure without taxonomic significance, its presence or absence largely depending on the developmental stage under investigation. As he puts it, "Damit verlieren die Hypothesen (Henckel), die *Tupaia* aus der Primatenreihe ausschliessen wollen, ihre Hauptstütze."¹ The placentation of tupaiids was very poorly known until quite recently. Meister and Davis (1956) have helped to fill this gap with their description of three stages in *Tupaia minor*. They conclude that "morphologically the placenta and other fetal membranes of *Tupaia* are almost an ideal starting point from which to derive the corresponding structures of the primates." Of particular interest for the present study is their further conclusion, based on comparison with Van der Horst's drawings (1950) of *Elephantulus*, that ". . . the placenta and fetal membranes in these two forms differ in almost every respect except placental type"; the data ". . . support the view that the tree-shrews and elephant shrews are not

¹ Since this was sent to press, W. Spatz' study of the ontogeny of the cranium of *Tupaia glis* (Morphol. Jahrb., 106: 321-416, 1964) has come to hand. He concludes that on this evidence tupaiids are primates.

closely related." The little evidence available on ectoparasites supports primate affinities for the former but not for the latter (Patterson, 1957, pp. 23, 26). A few uncertainties remain concerning the propriety of including tupaiids in the Primates. Some see the structure of the hand as a bar to inclusion while others do not. Buettner-Janusch and Buettner-Janusch (1964, p. 87) find that the electrophoretic behavior of the hemoglobin differs from that of other prosimians.¹ Jane, Campbell and Yashon (1965) have shown that in *Tupaia* the pyramidal tract occurs in the dorsal funiculus of the spinal cord, whereas in insectivores it occurs in the ventral funiculus and in primates in the lateral.² However, only one other prosimian, *Nycticebus*, has thus far been studied in this connection. A wider investigation may reveal that the distinction is not a clear cut one. It should be recalled, to introduce a note of caution, that until 1952 *Tupaia* could be said to differ from all primates in its possession of an outer bar of Jacobson's cartilage. In that year Eloff demonstrated the presence of the bar in *Galago senegalensis*. Certain facts do, of course, await further assessment, but the weight of the evidence now decidedly favors the ordinal reference; the burden of proof has shifted.

The Macroscelididae, to anticipate a little, are without much doubt a very ancient family that probably arose early in the Cenozoic, possibly even toward the end of the Mesozoic. In some respects specialized, they are nevertheless basically rather primitive. It is not surprising therefore that they should to varying degrees resemble other groups of mammals of more or less comparable antiquity. These resemblances, particularly those to the Insectivora and to the tupaiid primates, have been interpreted as indicative of close affinity to one or the other of these groups, wrongly interpreted I now believe.

As regards the soft anatomy, Le Gros Clark (1933, p. 1004) has stated of the brain that ". . . it would be difficult to conceive two small mammalian brains which are more fundamentally different and divergent in their structure than those of *Macroscelides* and *Tupaia*." Stephan and Spatz (1962) and Stephan and Andy (1964) also emphasize that the macroscelidid brain differs from those of Insectivora in various ways, notably in the much larger mesencephalon and hippocampus. The organ of Jacobson (Broom, 1902,

¹ On the basis of serum protein comparisons Goodman (1963, p. 137) concludes: "Although evidence for a definitive taxonomic assignment of the tree shrews has not been gathered, the serological data demonstrate that the tree shrews have affinities with the Primates. (Elephant shrews, placed by some taxonomists with tree shrews, do not show any primate or tupaiid affinities.)"

² In this, as in certain other respects, *Tupaia* may be simply primitive. The tract is dorsal in monotremes, marsupials, edentates and rodents.

1915) is of marsupial type, resembling that of *Tupaia* (presumably primitive in both groups) and very different from that of insectivores. Carlsson, although concluding that macroscelidids were close to erinaceids, did record certain characters in the musculature in which they resembled the tupaiids (1909, p. 396). The testes remain abdominal in elephant shrews, whereas the tree shrews have a well developed scrotum. Both, of course, have a caecum, but this is much larger in the elephant shrews. In sum, the evidence of the soft parts would appear to oppose close relationship to either the Tupaiidae or to the Insectivora.

The distinction between macroscelidids and tupaiids in placentation has been mentioned above (p. 324), as has the remarkable number of eggs liberated from the ovaries of certain of the Macroscelidinae (p. 307). The two families also differ as regards the young. In the elephant shrews these are decidedly precocial, being born fully haired, with the eyes open, and capable of active locomotion within a very short time (Hoesch and von Lehmann, 1956, p. 17; Walker *et al.* 1964, p. 135)¹. In tree shrews — and also in the Insectivora generally (Herter, 1957, p. 31) — this is not the case. Uterine bleeding has been described by Van der Horst (1954, and references there cited) in *Elephantulus "myurus,"* with the suggestion that this foreshadows the menstrual cycle of the higher primates. The bleeding is of an unusual type, however. During diestrus a polyp-like growth forms in one part of the uterus and disintegrates at the end of the stage; coiled arteries, which are "enormously developed," are confined to this part. In all likelihood this is simply another macroscelidid peculiarity.

The dentition of macroscelidids, particularly the posterior cheek teeth, is unlike that of any other group of mammals. Carlsson saw resemblances to the teeth of Erinaceidae, but these are not close. The Macroscelididae have at times been placed in the Insectivora "Dilambdodonta" although there is nothing whatsoever dilambdodont about their molars. Frechkop (1931) has stated that the cheek teeth resemble those of ungulates more than those of any other major group. This is correct — the myohyracines evolved molars so ungulate-like as to mislead some very competent students — but there is no detailed similarity to any particular group of

¹ A very curious observation concerning the young of *Elephantulus rupestris* has been reported. Fitzsimons (1920, pp. 12–13) quotes an observer, van Musschenbroek, who noticed that the two young "... were hanging on to something on top of the shoulder blades. On examination I found they were two teats, one on either side. [The mother] carried them by these teats [and] took good care to see that they were hanging on before she hopped away like a miniature kangaroo." As regards the position of the teats confirmation is supplied by Burton (1955), who states that Hayman found them to be situated high on the flanks just behind and above the scapulae.

hoofed mammals. The resemblance is an interesting example of convergence, as Friant (1935) concluded. On the basis of his observations, Frechkop asserted that the macroscelidids were on the ungulate road, just as the tupaiids were on the primate one. In this, of course, he went too far. All, or practically all, ungulate orders have surely emerged from the Condylarthra (to which the Arctocyonidae properly belong), and there is nothing suggestively condylarthran in the elephant shrews. Nevertheless, the myohyracines do raise the possibility that placental mammals could achieve "ungulate" grade independently of that order.¹ The dentition of the extinct macroscelidids gives no hint as to relations with any other group. The earliest known form, *Metoldobotes*, had the typical pattern and had lost the last molar.

The most recent study of the skeleton of the Macroscelididae is that of Evans (1942), who compared representatives of all genera except *Macroscelides* (see p. 309) with those of *Tupaia* and *Echinosorex*. He concluded that the macroscelidids resembled *Tupaia* in 30 osteological features and *Echinosorex* in 13. Further, he claimed that out of 40 lemuroid features mentioned by Gregory and by Carlsson as occurring in *Tupaia*, the macroscelidids shared in 32. This "simple morphological balance," as Simpson (1945, p. 176) called it, has been seized on as evidence for the reality of Menotyphla *sensu* Haeckel (e.g. Grassé, 1955, p. 1649; Heim de Balzac and Bourlière, 1955, p. 1691). It does not provide such evidence. Evans' study is in fact a classic example of the "rut discussions" mentioned above. He has shown beyond question that tupaiids and macroscelidids differ in a number of features, some of them more or less similar, from *Echinosorex*, which, as a true insectivore, has various characters not found in other major groups of mammals. This is a far cry from proving a close relationship between elephant shrews and tree shrews, however. Looking beyond the restricted prosimian-tupaiid-macroscelidid-insectivore circle, it becomes apparent at once that few of Evans' characters in common between tupaiids and macroscelidids are confined to these families. Furthermore, the resemblance between the two in many of the features cited is far from close. Some of the common features, e.g. the relatively large braincase, were in all probability independently acquired (the braincases at least house very dissimilar brains); others, e.g. the structure of the orbito-temporal region and of the zygomatic arch, are simply primitive eutherian, or therian, characters inherited by both; others again,

¹ The only other possible candidates for such a distinction that I can think of are the notoungulates. I am not suggesting a macroscelidid-notoungulate relationship!

e.g. the presence of a free centrale and of a third trochanter on the femur, are characters so widely possessed as to be meaningless in this context; yet others, e.g. large auditory bullae and slender coronoid process of the mandible, are not sufficiently similar structurally to qualify as significant resemblances; and so on. The same applies to the features cited as occurring in common between macroscelidids and lemuroids. Butler (1956, p. 476) has listed certain cranial characters in which the Macroscelididae, Dermoptera, Tupaiidae and Lemuroidea resemble each other. Some of these features are of the same sort as those cited by Evans. As regards the Macroscelididae, at least, they are equally open to question, as Butler recognized. The evidence from the hard parts seems to me to point in the same direction as that from the soft: namely, that the macroscelidids are sharply distinct from both Tupaiidae and Insectivora. Resemblances to ungulates do exist — *Rhynchocyon* and *Orycteropus* are remarkably similar in the disposition of the bones in the orbitotemporal region (cf. figs. 124 and 177 in Gregory, 1920), the rostral and caudal entotympanics of elephant shrews compare rather closely with those of notoungulates, fusion of distal elements in the limbs occurs in macroscelidids and in hoofed mammals, the astragalus has a fairly long neck in some small and primitive ungulates, etc. — but these appear to be either convergent or simply primitive in both.

Evans concluded, on the basis of superficial resemblances, that *Anagale* from the early Oligocene of Mongolia “. . . is, in many osteological features, intermediate between the Macroscelidae and the Tupaiidae and is either the common ancestor of the two families or quite close to it.” New evidence, derived from a hitherto undescribed specimen of *Anagale*, and from *Anagalopsis*, reveals that the cheek teeth are quite different from those of either family, and that the tympanic forms the lateral portion of the bulla instead of being a ring enclosed by the entotympanic, as Simpson (1931) had supposed. Basing his conclusion on this evidence and on the very peculiar structure of the unguis, McKenna (1963a) has removed the Anagalidae from the Tupaiioidea, where Simpson had placed them, and listed them as Eutheria *incertae sedis*. Whatever the anagalids may prove to be, they are not related to the macroscelidids. *Metoldobotes*, it may be recalled, was contemporary with *Anagale*.

As will by now be evident, I believe the elephant shrews to be a group of mammals distinct from both the Insectivora and the tupaiid primates. Their known distribution is exclusively African, and they make their first appearance in the record in the earliest

adequately known mammalian fauna of that continent. They are accompanied there by an array of mammalian groups unknown elsewhere in deposits of earlier or similar date — hyracoids, arsinotheres, moeritheres, barytheres, proboscideans and catarrhine primates. So notable a degree of endemism argues a long isolation of Africa¹ (Darlington, 1957, pp. 365, 590; Patterson, 1957, p. 45), one lasting throughout much of the Eocene at least. Macroscelidids may well have been members of this "old African" fauna, survivors from the later Cretaceous beginnings of the Eutheria. As a group they are more diversified and contain more genera than almost one-third of the currently recognized orders of eutherian mammals. They are, I believe, worthy of ordinal rank.

Butler (1956) has proposed for them the ordinal name Macroscelidea² without definition. Such action seems preferable to restriction of Menotyphla to the elephant shrews. Menotyphla has long had a proto-primate flavor, and since the tupaiid half of the artificial assemblage almost surely is primate and the macroscelidid half assuredly is not, it hardly seems desirable to attempt perpetuation of so ambiguous a name for the latter alone.

The order may be defined as follows:

MACROSCELIDEA

Dentition I_{3-3}^{0-3} , C_1^1 , P_4^4 , M_{2-3}^{2-3} ; P_4^4 large, molariform; upper cheek teeth without mesostyles; M_3^3 , when present, greatly reduced; posterior cheek teeth brachyodont to hypsodont. Skull with complete zygomatic arch; orbits large, open posteriorly; maxilla not extending into orbital wall, palatine with orbital wing; auditory bulla compound, ectotympanic, rostral and caudal entotympanics, alisphenoid, squamosal, periotic participating; mandible with high ascending ramus, condyle well above level of cheek teeth, coronoid process small. Pelvis with pubic symphysis; humerus with entepicondylar foramen; distal segments of legs longer than proximal; radius and ulna fused or closely appressed, tibia and

¹ When this isolation began and ended is of course uncertain. Darlington, on the basis of the rather few northern forms that occur in the Fayum deposits, believes that a connection had by then become established. This does not seem certain; that only two or three of a great many northern groups would have made their way over a land bridge had this been fully in existence is rather unlikely. The Fayum rodents belong to a family not known in Eurasia; they may well have descended from waif ancestors transported during the period of isolation.

² Somewhat vaguely, however, since in the body of his paper (p. 479) he expressed doubt as to the propriety of including the elephant shrews in the Insectivora ("Lipotyphla" in his terminology), suggesting that they should either "... be included in the Primates as an outlying suborder, or a new order, Macroscelidea, should be created for them." In the summary (p. 480) he simply remarked that they are "... placed in a new order, Macroscelidea." Haeckel's prior — and invalid (by modern standards) — use of the same name for the family does not constitute preoccupation. I was previously dubious about recognition of the order (1957, p. 23), but with the increase in knowledge of the fossil record my doubts have disappeared.

fibula fused; pollex and hallux reduced or absent; astragalar neck moderately long. Proboscis long, flexible; organ of Jacobson of marsupial type; brain with relatively large mesencephalon and specialized hippocampus; caecum relatively large; testes abdominal.

One family, Macroscelididae, with four subfamilies: Macroscelidinae, Rhynchoeyoninae, Mylomygalinae, Myohyracinae.

Known range: Early Oligocene to Recent, Africa.

SUMMARY

The Macroscelididae, a wholly African group so far as known, includes four subfamilies, two of which are extinct. The Macroscelidinae date from the early Oligocene of the Fayum, where they are represented by *Metoldobotes*, a form originally referred to the insectivore family Mixodectidae. *Palaeothentoides* of the early Pleistocene(?), first described as a marsupial, is a valid member of the subfamily. Extinct species of *Elephantulus* are known from the Pleistocene. The early Miocene *Rhynchoeyon clarki* provides the only fossil record of the Rhynchoeyoninae. The subfamily Mylomygalinae is proposed for the Pleistocene *Mylomygale*, a remarkable form with hypsodont posterior cheek teeth convergent toward those of various rodents. The Myohyracinae, hitherto placed in the Hyracoidea as Myohyracidae or Myohyracoidea, are represented by the early Miocene *Myohyrax* and *Protypotheroides*. Their posterior cheek teeth are decidedly ungulate-like and comparable in complexity and degree of hypsodonty to those of Equinae and hypsodont Notoungulata. *Pseudorhynchoeyon cayluxi* from the Querey Phosphorites is not a member of the family.

The extinct subfamilies were beyond doubt predominantly herbivorous. Some evidence indicates that the surviving forms are to a degree omnivorous.

The affinities of the family are reviewed and the conclusion reached that macroscelidids are not closely related either to the tupaïid primates or to the insectivores. Resemblances to ungulates are either convergent or primitive. Butler's order Macroscelidea is recognized for the reception of the group and a definition is offered.

REFERENCES CITED

ANDREWS, C. W.

1914. On the lower Miocene vertebrates from British East Africa collected by Dr. Felix Oswald. Quart. Jour. Geol. Soc. London, **70**: 163-186.

- BROOM, R.
1898. On the affinities and habits of *Thylacoleo*. Proc. Linn. Soc. New South Wales, **23**: 57-74.
1902. On the organ of Jacobson in the elephant-shrew (*Macroscelides proboscideus*). Proc. Zool. Soc. London, 1902: 224-228.
1915. On the organ of Jacobson and its relations in the "Insectivora" — Part I. *Tupaia* and *Gymnura*. *Ibid.*, 1915: 157-162.
1937. On some new Pleistocene mammals from limestone caves of the Transvaal. South Afr. Jour. Sci., **33**: 750-768.
1938. Note on the premolars of the elephant shrews. Ann. Transvaal Mus., **19**: 251-252.
1948. Some South African Pliocene and Pleistocene mammals. *Ibid.*, **21**: 1-38.
- BROOM, R. and G. W. H. SCHEPERS
1946. The South African fossil ape-men, the Australopithecinae. Mem. Transvaal Mus., No. 2: 1-272.
- BUETTNER-JANUSCH, J. and V. BUETTNER-JANUSCH
1964. Hemoglobins of Primates. In Evolutionary and genetic biology of Primates, ed. J. Buettner-Janusch. Vol. 2, pp. 75-90. New York and London: Academic Press.
- BURTON, M.
1955. Elephant shrews. Illus. London News, **226**: 412.
- BUTLER, P. M.
1956. The skull of *Ictops* and the classification of the Insectivora. Proc. Zool. Soc. London, **126**: 453-481.
- BUTLER, P. M. and A. T. HOPWOOD
1957. Insectivora and Chiroptera from the Miocene rocks of Kenya Colony. Brit. Mus. (Nat. Hist.). Fossil Mammals of Africa, No. 13: 1-35.
- CARLSSON, A.
1909. Die Macroscelidae und ihre Beziehungen zu den übrigen Insectivoren. Zool. Jahrb., Abt. Syst. Ökol. Geogr. Tiere, **28**: 349-400.
1922. Über die Tupaiidae und ihre Beziehungen zu den Insectivora und den Prosimiae. Acta Zool., **3**: 227-270.
- DARLINGTON, P. J., JR.
1957. Zoogeography, the geographical distribution of animals. New York: John Wiley and Sons, Inc., pp. i-xiii, 1-675.
- ELLERMAN, J. R., T. C. S. MORRISON-SCOTT and R. W. HAYMAN
1953. Southern African mammals 1758 to 1951: a reclassification. London: British Museum (Natural History), pp. 1-363.
- ELOFF, F. C.
1952. On the organ of Jacobson and the nasal floor cartilages in the chondrocranium of *Galago senegalensis*. Proc. Zool. Soc. London, **121**: 651-655.
- EVANS, F. G.
1942. Osteology and relationships of the elephant shrews (*Macroscelididae*). Bull. Amer. Mus. Nat. Hist., **80**: 85-125.

- FIEDLER, W.
1953. Die Kaumuskulatur der Insectivora. *Acta Anat.*, **18**: 101-175.
- FILHOL, H.
1892. Note sur un insectivore nouveau. *Bull. Soc. Philom.*, (8) **4**: 134.
- FITZSIMONS, F. W.
1920. The natural history of South Africa. Mammals. Vol. IV. London: Longmans, Green and Co., pp. i-xix, 1-271.
- FRECHKOP, S.
1931. Note préliminaire sur la dentition et la position systématique des Macroscelidæ. *Bull. Mus. Roy. Hist. Nat. Belg.*, **7** (6): 1-11.
- FRIANT, M.
1935. La morphologie des dents jugales chez les macroscelididés. *Proc. Zool. Soc. London*, 1935: 145-153.
- GOBERT, E.
1912. L'abri de Redeyef. *L'Anthropologie*, **23**: 151-168.
- GOODMAN, M.
1963. Serum protein comparisons by two-dimensional starch-gel electrophoresis and immunodiffusion plate reactions applied to the systematics of primates and other mammals. *Proc. XVI Internat. Congr. Zool.*, **4**: 133-142.
- GRASSÉ, P.-P.
1955. Ordre des insectivores. Anatomie et reproduction. Affinités zoologiques des diverses familles entres elles et avec les autres ordres de mammifères. *In* *Traité de Zoologie*, P.-P. Grassé ed. Paris: Masson et Cie. Vol. 17, Mammifères, fasc. 2: 1574-1653.
- GREGORY, W. K.
1910. The orders of mammals. *Bull. Amer. Mus. Nat. Hist.*, **27**: 1-524.
1920. Studies in comparative myology and osteology: No. IV. A review of the evolution of the lacrymal bone of vertebrates with special reference to that of mammals. *Ibid.*, **42**: 95-263.
- HAECKEL, E.
1866. *Generelle Morphologie der Organismen*. Berlin: Georg Reimer, Vol 2. Pp. i-cix, 1-462.
- HEIM DE BALSAC, H. and F. BOUILLÈRE
1955. Ordre des insectivores. Systématique. *In* *Traité de Zoologie*, P.-P. Grassé, ed. Paris: Masson et Cie. Vol. 17, Mammifères, fasc. 2: 1653-1697.
- HENCKEL, K. O.
1928. Das Primordialeranium von *Tupaia* und der Ursprung der Primaten. *Zeitschr. Anat. Entwickl.*, **86**: 201-227.
- HERTER, K.
1957. Das Verhalten der Insectivoren. *In* *Handbuch der Zoologie*, J.-G. Helmeke, H. von Lengerken and D. Starek, eds. Berlin: Walter de Gruyter u. Co. Bd. 8, lief. 9, 10(10): 1-50.
- HOESCH, W. and E. VON LEHMANN
1956. Zur Säugetier-Fauna Südwestafrikas. *Bonn. Zool. Beitr.*, **7**: 8-57.

- HOPWOOD, A. T.
1929. New and little-known mammals from the Miocene of Africa. Amer. Mus. Novit., No. 344: 1-9.
- JANE, J. A., C. B. G. CAMPBELL and D. YASHON
1965. Pyramidal tract: a comparison of two prosimian primates. Science, **147**: 153-155.
- LE GROS CLARK, W. E.
1933. The brain of the Insectivora. Proc. Zool. Soc. London, 1932: 975-1013.
1934. Early forerunners of man. A morphological study of the evolutionary origin of the primates. London and Baltimore: Balliere, Tindall and Cox, William Wood and Co. Pp. i-xvi, 1-296.
1959. The antecedents of man. An introduction to the evolution of the Primates. Edinburgh: The University Press. Pp. i-ix, 1-374.
- McKENNA, M. C.
1963a. New evidence against tupaoid affinities of the mammalian family Anagalidae. Amer. Mus. Novit., No. 2158: 1-16.
1963b. Primitive Paleocene and Eocene Apatemyidae (Mammalia, Insectivora) and the primate-insectivore boundary. *Ibid.*, No. 2160: 1-39.
- MATTHEW, W. D.
1910. Schlosser on Fayum mammals. A preliminary notice of Dr. Schlosser's studies upon the collection made in the Oligocene of Egypt for the Stuttgart Museum by Herr Markgraf. Amer. Nat., **49**: 700-703.
1915. A revision of the Wasatch and Wind River faunas. Part IV—Entelonychia, Primates, Insectivora (part). Bull. Amer. Mus. Nat. Hist., **34**: 429-483.
- MEISTER, W. and D. D. DAVIS
1956. Placentation of the pygmy treeshrew. Fieldiana: Zool., **35**: 71-84.
- PATTERSON, B.
1957. Mammalian phylogeny. In Première symposium sur la spécificité parasitaire des parasites des vertébrés. Neuchâtel: Paul Aldinger. Pp. 15-48.
- PETERS, W.
1864. Ueber die Säugethier-Gattung *Solenodon*. Abh. K. Akad. Wiss. Berlin, 1863: 1-22.
- ROMER, A. S.
1928. Pleistocene mammals of Algeria. Fauna of the Paleolithic station of Mechta-el-Arbi. Bull. Logan Mus., **1**: 80-163.
- ROUX, G. H.
1947. The cranial development of certain Ethiopian insectivores and its bearing on the mutual affinities of the group. Acta Zool., **28**: 165-307.
- SABAN, R.
1956- Les affinités du genre *Tupaia* Raffles 1821, d'après les caractères morphologiques de la tête osseuse. Ann. Paléont., **42**: 169-224 (1956); **43**: 1-44 (1957).

SCHLOSSER, M.

1910. Über einige fossile Säugetiere aus dem Oligocän von Ägypten. Zool. Anz., **35**: 500-508.
1911. Beiträge zur Kenntnis der oligozänen Landsäugetiere aus dem Fayum, Ägypten. Beitr. Pal. Geol. Österr.-Ungar. Orients, **24**: 51-167.

SCLATER, W. L.

1901. The mammals of South Africa. Vol. II. Rodentia, Chiroptera, Insectivora, Cetacea and Edentata. London: R. H. Porter. Pp. i-xii, 1-241.

SHORTTRIDGE, G. C.

1934. The mammals of South West Africa. A biological account of the forms occurring in that region. Vol. I. Pp. i-xxv, 1-437. London: William Heinemann Ltd.

SIMPSON, G. G.

1931. A new insectivore from the Oligocene, Ulan Gochu horizon, of Mongolia. Amer. Mus. Novit., No. 505: 1-22.
1935. The Tiffany fauna, upper Paleocene. II. Structure and relationships of *Plesiadapis*. *Ibid.*, No. 816: 1-30.
1945. The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist., **85**: i-xvi, 1-350.

SATRICK, D.

1960. Das Cranium eines Schimpansenfetus (*Pan troglodytes* [Blumenbach 1799]) von 71 mm SchStlg., nebst Bemerkungen über die Körperform von Schimpansenfeten. (Beitrag zur Kenntnis des Primatencraniums II). Morphol. Jahrb., **100**: 559-647.
1932. Das Cranium von *Propithecus* spec. (Prosimiae, Lemuriformes, Indriidae). (Beiträge zur Kenntnis des Primaten-Craniums III). Bibl. primat., **1**: 163-196.

STEPHAN, H. and O. J. ANDY

1964. Quantitative comparisons of brain structures from insectivores to primates. Amer. Zool., **4**: 59-74.

STEPHAN, H. and H. SPATZ

1962. Vergleichend-anatomische Untersuchungen an Insectivorengehirnen. IV, Gehirne afrikanischer Insectivoren. Versuch einer Zuordnung von Hirnbau und Lebensweise. Morphol. Jahrb., **103**: 108-174.

STROMER, E.

1922. Erste Mitteilung über tertiäre Wirbeltier-Reste aus Deutsch-Südwestafrika. Sitzungsber. math.-phys. Kl. Bayer. Akad. Wiss., 1921: 331-340.
1926. Reste Land- und Süßwasser-bewohnender Wirbeltiere aus den Diamantfeldern Deutsch-Südwestafrikas. In Kaiser, E., Die Diamantenwüste Südwestafrikas, vol. 2. Pp. 107-153. Berlin: Dietrich Reimer.
1931. Reste Süßwasser und Land bewohnender Wirbeltiere aus den Diamantfeldern Klein-Namaqualandes (Südwestafrika). Sitzungsber. math.-nat. Abt. Bayer. Akad. Wiss., 1931: 17-47.

1932. *Palacothentoides africanus* nov. gen., nov. spec., ein erstes Beuteltier aus Afrika. *Ibid.*, 1931: 177-190.
- THOMAS, O.
1901. List of small mammals obtained by Mr. A. E. Pease, M.P., during his recent expedition to Abyssinia, with descriptions of three new forms of *Macrosclides*. *Ann. Mag. Nat. Hist.*, (7) 8: 154-156.
1913. List of mammals obtained by the Hon. Walter Rothschild, Ernst Hartert and Carl Hilgert in western Algeria during 1913. *Novit. Zool.*, 20: 586-591.
- THOMAS, O. and H. SCHWANN
1906. The Rudd exploration of South Africa. V. List of mammals obtained by Mr. Grant in N. E. Transvaal. *Proc. Zool. Soc. London*, 1906: 575-591.
- VAN DER HORST, C. J.
1944. Remarks on the systematics of *Elephantulus*. *Jour. Mammal.*, 25: 77-82.
1950. The placentation of *Elephantulus*. *Trans. Roy. Soc. S. Afr.*, 32: 435-629.
1954. *Elephantulus* going into anoestrus: menstruation and abortion. *Phil. Trans. Roy. Soc. London*, 238 B: 27-61.
- VAN DER KLAUW, C. J.
1929. On the development of the tympanic region of the skull in the Macrosclididae. *Proc. Zool. Soc. London*, 1929: 491-560.
- WAGNER, P. A. and H. MERENSKY
1929. The diamond deposits on the coast of Little Namaqualand. With an appendix on the palaeontology of the Namaqualand coastal deposits by S. H. Haughton. *Trans. Geol. Soc. S. Afr.*, 31: 1-41.
- WALKER, E. P., F. WARNICK, K. I. LANGE, H. E. UIBLE, S. E. HAMLET, M. A. DAVIS and P. F. WRIGHT
1964. *Mammals of the world*. Vol. 1. Pp. i-1, 1-644. Baltimore: The Johns Hopkins Press.
- WHITWORTH, T.
1954. The Miocene hyracoids of East Africa. *Brit. Mus. (Nat. Hist.) Fossil Mammals of Africa*, No. 7: 1-58.
1958. Miocene ruminants of East Africa. *Ibid.*, No. 15: 1-50.

(Received 19 February 1965.)